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Changes in nutrient uptake and utilization by rice under simulated climate change conditions: A 2-year experiment in a paddy field

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ABSTRACT

Global climate change with elevated atmospheric CO_2 concentration and temperature has been known impacting plant photosynthesis and grain yield in agroecosystems. However, how nutrient uptake and utilization by rice change under climate change stresses has been poorly addressed. An open-air field experiment was conducted to investigate the impacts of factorial combinations of CO_2 enrichment (up to 500 ppm) and canopy warming (+2 °C) on nutrient concentration (PNC), accumulation (PNA) and utilization efficiency (NUE) for two cropping years in a paddy from southeast China. Plant samples of aboveground biomass were collected across the growing stages and grain yield measured at harvest. Compared to ambient condition, CO_2 enrichment more or less decreased PNC of N, P and K, but unchanged PNA of N and P while increased aboveground biomass. In contrast, warming increased PNC of N, P and K respectively by 7.4%, 11.0% and 13.4% at the ripening stage, but decreased PNA of N, P and K respectively by 18.6%, 22.6% and 10.8% in 2013. Whereas, concurrent CO_2 enrichment and warming unchanged PNC but slightly decreased PNA of N and K in both years. In addition, CO_2 enrichment unchanged the apparent NUE, but increased NUE of N and K under concurrent warming in both years. Therefore, canopy warming may have impacted the rice response in NUE to CO_2 enrichment as the change in PNA with concurrent CO_2 enrichment and warming was in a similar trend to that with warming alone. Our findings suggest that nutrient uptake and utilization by rice are more impacted by warming compared with CO_2 enrichment under the simulated climate change conditions. Therefore, simulated climate change experiments should be conducted regarding how simultaneous atmospheric CO_2 enrichment and warming influences plant traits and functions in rice paddy, to provide a better understanding of agricultural production changes and sustainable nutrient management under future climate change.

1. Introduction

The global atmospheric carbon dioxide (CO_2) concentration has increased by 40% since the pre-industrial time and surface temperature has increased by 0.85 °C during 1880–2012, resulting from the anthropogenic greenhouse gas emissions from land use change and fossil fuel combustion (IPCC, 2013). These characteristics of climate change have exerted both direct effects on crop growth and production (Wang et al., 2016a; Wheeler and von Braun, 2013) and indirect effects on plant nutrient uptake and utilization (Cheng et al., 2010; Lam et al., 2012a). Elevated atmospheric CO_2 concentration generally increases crop yield through enhanced photosynthesis (Horie et al., 2000; Kim et al., 2003; Mitchell et al., 1993; Sakai et al., 2006), while warming reduces dry matter accumulation via increased plant respiration and accelerated phenological development (Bhattacharyya et al., 2014; Dong et al., 2011; Wheeler et al., 2000). While nutrient balance and utilization are known central to the impact of climate change on crop production (Fuhrer, 2003; Lam et al., 2012b; Wheeler and von Braun, 2013), the response of crop in agroecosystems to concurrent CO_2 enrichment and warming has not yet been sufficiently addressed.

Rice (*Oryza sativa*) is one of the most important staple crops for more than half of the world population (Nagai and Makino, 2009). About one quarter of the croplands of China are cultivated for rice production, accounting for about 20% to the world total rice area (Frolking et al., 2002). Rice grain production could be enhanced by 11–19% under atmospheric CO_2 enrichment (Long et al., 2006), which could be potentially negated by concurrent warming (Wang et al., 2016a). Such a change could be partly attributed to changes in nutrient

Abbreviations: PNC, plant nutrient concentration; PNA, plant nutrient accumulation; NUE, nutrient utilization efficiency

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dynamics in the soil and plant system. Furthermore, soil food web (Okada et al., 2014) and nitrification processes (Hu et al., 2016) were more impacted by elevated temperature compared with elevated CO_2 concentration. So far, it remains unclear whether the impacts of warming outweigh the effects of elevated CO_2 concentration on nutrient uptake and utilization in rice production.

Uptake and utilization of nitrogen (N), phosphorus (P) and potassium (K), as the major essential plant nutrients, are recognized as the most important abiotic factors for crop physiological function and production capacity. Changes in concentrations, uptake and utilization efficiency of these nutrients in agroecosystems have been addressed using experiments with atmospheric CO_2 enrichment or warming alone (Bloom et al., 2010; Jin et al., 2012; Li et al., 2015; Ma et al., 2007; Nam et al., 2013; Roy et al., 2012). A decrease in plant nutrient concentration (PNC) under elevated CO_2 was generally attributed to an increase in biomass, the so-called dilution effect (Conroy, 1992; Gifford et al., 2000; Pang et al., 2006; Yang et al., 2007). Despite a reduction in PNC, plant nutrient accumulation (PNA) was increased under elevated CO_2 as a function of the increase in biomass (Pang et al., 2006; Roy et al., 2012). Moreover, a change in transpiration under CO_2 enrichment or warming could modify the nutrient transfer by water transported from belowground (Jauregui et al., 2015; McGrath and Lobell, 2013; Wang et al., 2018). As shown in a recent study with winter wheat, warming significantly increased PNC of micronutrients, and stimulated their translocation from root to shoot (Wang et al., 2016b). In contrast, Pregitzer and King (2005) reported that warming decreased PNC of N in root and shoot of rice. To date, the effect of climate change (CO_2 enrichment and warming) on nutrient uptake by rice is not well understood.

The main objective of this study was to examine the changes in PNC, PNA and nutrient utilization efficiency (NUE) of N, P and K in a rice paddy field under simulated climate change conditions. We hypothesize that CO_2 enrichment may decrease PNC but increase PNA and NUE, while warming could increase PNC decrease NUE, mainly due to the changes in biomass production; We also hypothesize that concurrent CO_2 enrichment and warming may overall increase PNC but decrease NUE, potentially due to the stronger negative effect by warming on biomass production. We aim to provide knowledge for improving nutrient management in agriculture tackling future climate change.

2. Materials and methods

2.1. Site description

This study was conducted with a simulated climate change system in an experimental station of the Institute of Resource, Ecosystem and Environment of Agriculture (IREEA), Nanjing Agricultural University. This system was built on a rice farm in Kangbo Village (31°30′N, 120°33′E), Guli Township, Changshu Municipality Jiangsu Province, China. The soil is a typical rice paddy soil classified as Gleyic Stagnic Anthrosol formed on clayey lacustrine deposit. The topsoil has a pH (H_2O) of 7.0, soil organic carbon of 19.2 g kg^{-1}, total N of 1.3 g kg^{-1}, total P of 0.9 g kg^{-1}, total K of 15.0 g kg^{-1}, and the bulk density is 1.2 g cm^{-3}. The soil texture is clayey loam with 33.8% sand, 38.6% silt and 27.6% clay. The minimum, maximum and mean temperature over the whole rice growing season were 23.7 °C, 31.3 °C and 27.0 °C in 2013, and 21.2 °C, 28.1 °C and 24.2 °C in 2014, respectively. The total rainfall over the rice growing season were 567 mm and 804 mm respectively in 2013 and 2014.

The operational procedures of the facility were described in Wang et al. (2016a) and Liu et al. (2015). In brief, the system was designed based on two factorial combination of climate change conditions, including an atmospheric CO_2 enrichment up to 500 ppm (CE), a warming of canopy air by 2 °C (WA), and a concurrent atmospheric CO_2 enrichment and warming (CW), compared to ambient condition (CK). Each treatment plot was performed in an octagonal ring with a diameter of 8 m (a total plot area of *ca* 50 m^2) and replicated in triplicates. The treatment rings were separated by an in-between spacing of 28 m at least to avoid potential CO_2 contamination across the treatment areas. The actual average CO_2 enrichment and temperature increment were 535 ± 21 ppm and 1.8 ± 0.7 °C in 2013, and 505 ± 18 ppm and 1.6 ± 0.4 °C in 2014, respectively. The performance and maintenance of these treatments were carefully managed with a monitoring and adjusting facility throughout the rice growing period of both years.

2.2. Crop cultivation and fertilizer management

Rice was a japonica hybrid cultivar (*Oryza sativa* L. cv. Changyou No. 5) transplanted with 3 seedlings per hill and 26 hills per m^2 (15.3 cm × 25.4 cm for each hill) on 23rd June 2013 and 20th June 2014, and harvested on 29th October 2013 and 1st November 2014, respectively.

Farm management was carried out following local agronomic practices. Nitrogen was applied as urea (46% N) at 86 kg N ha^{-1} as basal fertilizer (incorporated at 10 cm depth) and at 69 kg N ha^{-1} as topdressing. A compound fertilizer of N-P_2O_5-K_2O (15-15-15, %) was applied at 375 kg ha^{-1} as topdressing after heading. Paddy rice was irrigated with the regimes of continuous flooding with drainage twice during mid-season of rice growing.

2.3. Plant sampling and analysis

Aboveground biomass (shoot plus grain) were collected at each treatment plot respectively at the jointing, heading and ripening stages in accordance with the phenological development subject to the climate change treatment. After washing with distilled water, the collected samples were oven-dried at 105 °C for 30 min and then at 70 °C until constant weight. All the plant samples were weighed and then ground to pass of 0.25 mm sieve prior to analysis. Plant samples were pretreated with H_2SO_4-H_2O_2 and the resultant mixture was heated in an electric heating plate at 550 °C for 4 h. Subsequently, the concentration of N was analyzed by the Kjeldahl digestion method (Bremner and Mulvaney, 1982). The P concentration was analyzed by spectrophotometry (TU-1810, Beijing Purkinje General Instrument Co., Ltd., China), and K concentration by flame photometer (FP6410, INESA, China).

Grain yield was measured in this study to estimate the NUE. All of the grain ears in each ring was collected in the ripening stage and weighted, and then threshed by portable thresher. Three random subsamples of grain were air-dried to measure the water content in rice grain (105 °C for 30 min, then 70 °C for 24 h).

2.4. Statistical analysis

N, P and K utilization (assimilation) efficiency represents the amount of grain produced by per unit of N, P and K up-taken by plant till harvest (Xu et al., 2012). Thus, the NUE of N, P and K could be calculated with the following equation:

$$NUE = \frac{Grain\ yield}{Nutrient\ accumulation}$$

Where, the NUE (g g^{-1}) is the grain yield (g m^{-2}) per unit of nutrient uptaken (g m^{-2}) by rice till harvest, either of N, P and K.

All data were expressed as means with standard deviation of three replicates. One-way ANOVA followed by Duncan's test was used to test the differences between treatments. The general linear mixed (GLM) model was conducted to analyze the major effects of CO_2 enrichment, warming, cropping season and their interactions on nutrient uptake and their utilization efficiency. All statistical analyses were carried out using IBM SPSS ver. 20.0. A difference was considered significant at a probability level $p < 0.05$.

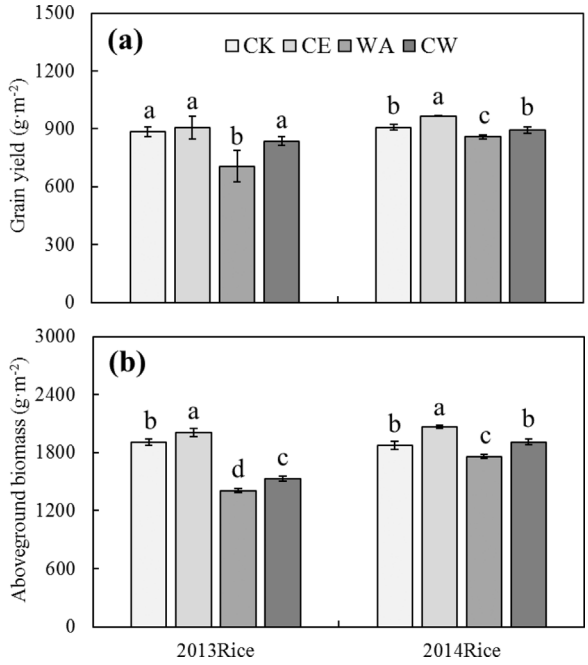

Fig. 1. Grain yield and aboveground biomass in both cropping seasons in response to CO_2 enrichment and warming. CK, untreated condition; CE, atmospheric CO_2 enrichment up to 500 ppm; WA, warming of canopy air by 2 °C; CW, simultaneous atmospheric CO_2 enrichment and warming. Different letters indicate significant differences between treatments at $p < 0.05$ by Duncan's test.

3. Results

3.1. Grain yield and aboveground biomass

As shown in Fig. 1, grain yield ranged from 706 to 885 g m^{-2} in 2013, and varied from 859 to 966 g m^{-2} in 2014. Compared to CK, CE significantly increased grain yield by 6.4%, but unchanged in 2013. In contrast, WA reduced grain yield by 20.3% in 2013, but by 5.4% in 2014. However, CW unchanged grain yield compared to CK in both years.

Aboveground biomass production ranged in 1407 to 2009 g m^{-2} in 2013, and changed from 1758 to 2064 g m^{-2} in 2014 (Fig. 1). Compared to CK, CE significantly increased aboveground biomass by 5.3% in 2013 and 10.1% in 2014. In contrast, WA decreased aboveground biomass by 26.2% in 2013 and 6.2% in 2014. However, aboveground biomass was decreased by 19.7% in 2013, but unchanged in 2014 under CW, relative to CK. There was no significant interaction in aboveground biomass between CO_2 and warming (Table 1).

3.2. Plant nutrient concentration

The PNC of N in the ripening stage was decreased under CO_2 enrichment (CE and CW), on average, by 4.4% in 2013 and 10.3% in 2014 (Table 2). In contrast, warming (WA and CW) increased PNC of N by 7.4% ripening stage of 2013, and by 12.4% at the jointing stage of 2014. However, CW generally had no significant effect on PNC of N compared to CK (Fig. 2a). Furthermore, a significant interaction between CO_2 enrichment and warming was observed at the jointing and ripening stages in 2014, but not in 2013.

Similarly, the PNC of P was decreased respectively by 42.2% and 28.1% under CE at the jointing and heading stages of 2014 compared to CK, though unchanged in 2013 (Fig. 2b). In contrast, warming (WA and CW) increased PNC of P by 11.0–14.9% across all stages in 2013 and by 24.2% at the heading stage in 2014. Also, there was no significant interaction between CO_2 enrichment and warming for PNC of P, except at the jointing stage in 2014.

Compared to CK, a decrease by 40.5% in PNC of K was observed under CE at the heading stage, but by 21.3% under CW at the ripening stage, in 2014 (Fig. 2c). Whereas, an increase in PNC of K was seen under warming (WA and CW) by 8.6–13.4% across the stages in 2013 and by 42.2% at the heading stage in 2014 (Table 2). There was no significant interaction between CO_2 enrichment and warming for PNC of K ($p > 0.05$), despite of a significant interaction only at the ripening stage in 2014 (Table 2).

3.3. Nutrient accumulation and utilization efficiency

Total PNA, as a function of the concentration and biomass production, varied among the treatments (Fig. 3). In 2013, PNA of N was significantly decreased by 18.6% under WA and by 17.5% under CW, compared to CK. However, PNA of P was significantly reduced under WA by 22.6% in 2013. Whereas, PNA both of N and P were unchanged under CE in both years. Compared to CK, PNA of K was unchanged under WA, increased under CE by 16.5%, but decreased under CW by 19.9% in 2014. Moreover, under CW, PNA of all the major elements were seen decreased, but the degree was dependent on the years.

Compared to CK, CE and WA generally unchanged NUE of N and K in both years (Fig. 4). However, CW increased NUE of N by 14.4% in 2013, and NUE of K by 21.8% in 2014. By contrast, NUE of P was unchanged under simulated climate change conditions in both years.

4. Discussions

4.1. CO_2 enrichment effect on nutrient uptake and accumulation

Changes in PNC, PNU and NUE under CO_2 enrichment varied with elements and years (Tables 1 & Table 2). Nitrogen supply has been recognized as the most important factor in climate smart agriculture (Lipper et al., 2014). Indeed, a significant reduction in PNC of N under CO_2 enrichment was observed only in 2014, by an extent up to 10.3% in the ripening stage. Atmospheric CO_2 enrichment was also reported to significantly decrease the N concentration in grain and leaf of rice (Cheng et al., 2010). Kim et al. (2011) reported the PNC of N was

Table 1
Summary of the analysis of general linear mixed model of grain yield, aboveground biomass, nutrient accumulation and utilization efficiency.

Source	*df*	Grain yield	Aboveground biomass	PNA			NUE		
				N	P	K	N	P	K
CO_2	1	0.001	< 0.001	0.898	0.011	0.989	0.016	0.154	0.020
Warming	1	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.185	0.693	0.089
Year	1	< 0.001	< 0.001	< 0.001	< 0.001	0.204	0.003	< 0.001	0.160
CO_2*Warming	1	0.202	0.771	0.014	0.008	0.004	0.002	0.901	< 0.001
CO_2*Year	1	0.366	0.032	0.473	0.066	0.388	0.773	0.684	0.615
Warming*Year	1	0.061	< 0.001	0.035	0.243	0.893	0.243	0.450	0.136
CO_2*Warming*Year	1	0.052	0.248	0.037	0.146	0.058	0.766	0.799	0.228

Note: PNA, plant nutrient accumulation; NUE, nutrient utilization efficiency.

Table 2
Summary of the analysis of general linear mixed model of nutrient concentration.

Source	2013			2014		
	Jointing	Heading	Ripening	Jointing	Heading	Ripening
N concentration						
% Change by CO_2	−5.57	−4.06	−4.36	−15.44	−10.03	−10.28
% Change by warming	−0.38	3.57	7.41	12.36	10.88	1.09
CO_2	0.206	0.124	0.090	0.001	0.061	0.041
Warming	0.929	0.187	0.015	0.011	0.066	0.811
CO_2*Warming	0.282	0.126	0.238	< 0.001	0.564	0.028
P concentration						
% Change by CO_2	−4.68	1.51	−1.65	−17.70	−23.83	−7.41
% Change by warming	14.05	14.86	10.98	19.15	24.21	0.25
CO_2	0.275	0.782	0.714	0.112	0.001	0.271
Warming	0.012	0.033	0.040	0.148	0.001	0.981
CO_2*Warming	0.104	0.614	0.223	0.027	0.836	0.866
K concentration						
% Change by CO_2	−2.04	2.90	−4.31	8.90	−21.35	−12.14
% Change by warming	11.52	8.59	13.43	−8.06	42.15	−8.33
CO_2	0.286	0.433	0.367	0.259	0.020	0.021
Warming	< 0.001	0.044	0.026	0.266	0.003	0.089
CO_2*Warming	0.262	0.607	0.174	0.239	0.058	0.003

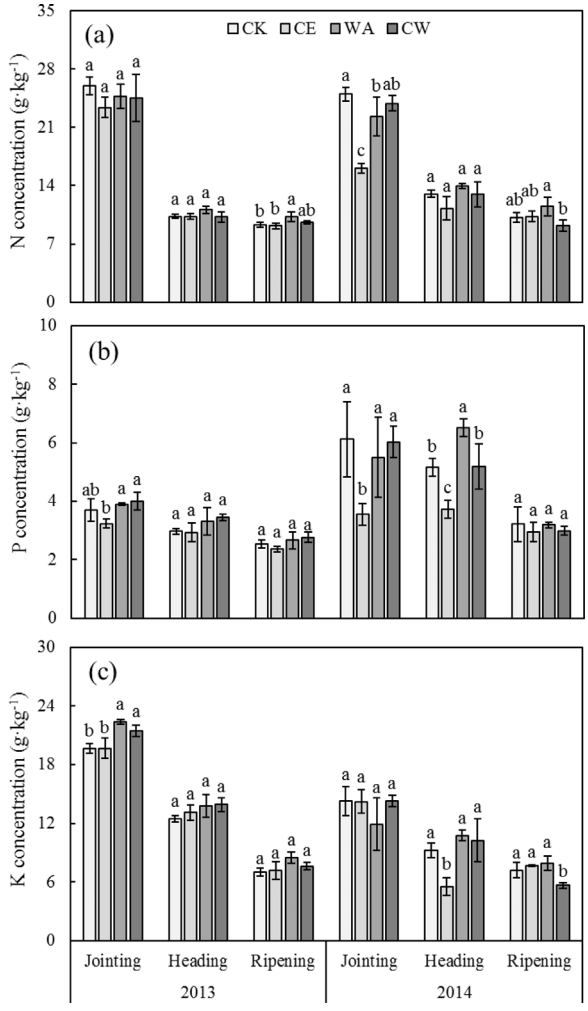

Fig. 2. Concentrations of N (a), P (b) and K (c) in both cropping seasons in response to CO_2 enrichment and warming. CK, untreated condition; CE, atmospheric CO_2 enrichment up to 500 ppm; WA, warming of canopy air by 2 °C; CW, simultaneous atmospheric CO_2 enrichment and warming. Different letters indicate significant differences between treatments at $p < 0.05$ by Duncan's test.

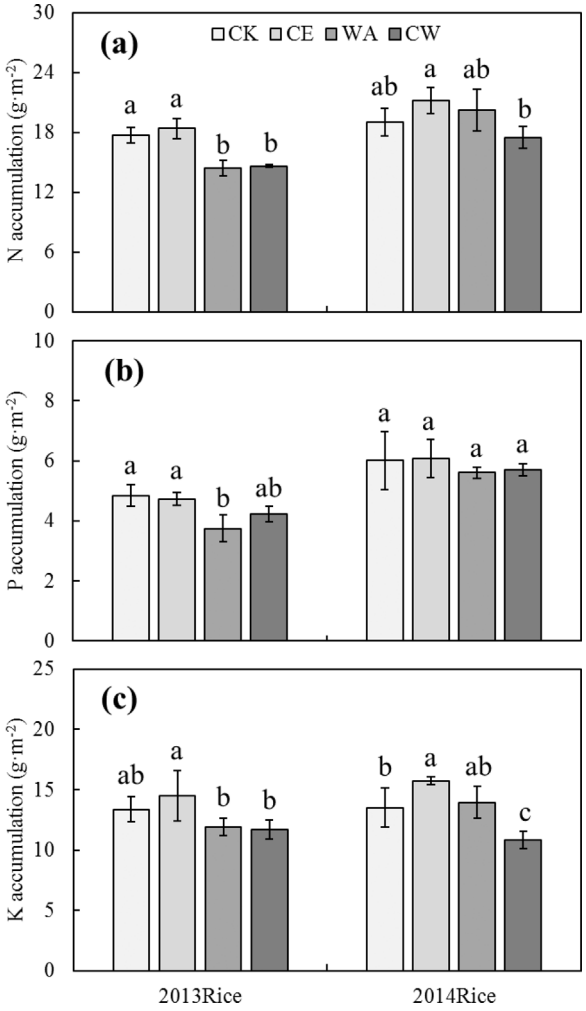

Fig. 3. Accumulations of N (a), P (b) and K (c) in both cropping seasons in response to CO_2 enrichment and warming. CK, untreated condition; CE, atmospheric CO_2 enrichment up to 500 ppm; WA, warming of canopy air by 2 °C; CW, simultaneous atmospheric CO_2 enrichment and warming. Different letters indicate significant differences between treatments at $p < 0.05$ by Duncan's test.

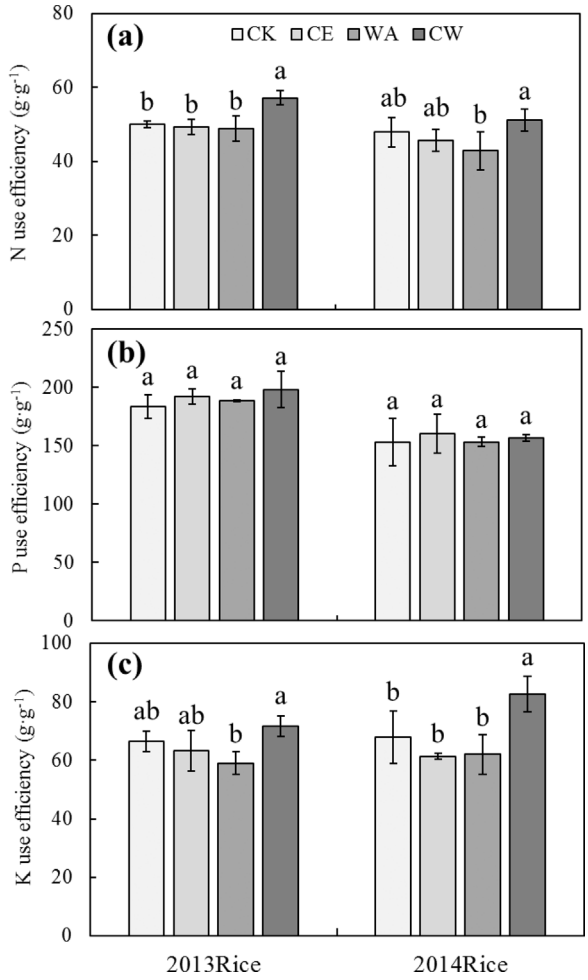

Fig. 4. Utilization efficiency of N (a), P (b) and K (c) in both cropping seasons in response to CO_2 enrichment and warming. CK, untreated condition; CE, atmospheric CO_2 enrichment up to 500 ppm; WA, warming of canopy air by 2 °C; CW, simultaneous atmospheric CO_2 enrichment and warming. Different letters indicate significant differences between treatments at $p < 0.05$ by Duncan's test.

decreased by 15.8% in a field experiment of rice paddy. Such a decrease was often attributed to a dilution effect of increased C assimilation under CO_2 enrichment (Coleman et al., 1993; Norby et al., 1999). That could be partially explained by the increased aboveground biomass under CE treatment (Fig. 1 b). However, Lam et al. (2012b) argued that a dilution effect of N concentration may not account for such a reduction in PNC of N in wheat plant under CO_2 enrichment supplied with enough exotic N inputs. In addition, plant pysiological functions may be subject to cliamte change condition. A decline in stomatal conductance and transpiration rate was often observed under treatment of atmospheric CO_2 enrichment, potentially limiting nutrient transport from belowground and thus reduces nutrient concentrations in plant tissues (Houshmandfar et al., 2015; Jauregui et al., 2015; Li et al., 2015; Pang et al., 2006; Wang et al., 2018); Finally, changes in plant photorespiration (Bloom et al., 2014; Jauregui et al., 2015) and in NO_3^- assimilation in the shoot of C_3 plants (Bloom et al., 2010) may also affect the N concentration in rice plant. Unfortunately, a quantification of these effects was not allowed in this study.

Plant concentrations of P and K were generally unchanged under CO_2 enrichment across stages in 2013. By contrast, a negative change in PNC occurred in the heading stage for both P and K, and in the ripening stage for K, in 2014. Changes in PNC of P and K with CO_2 enrichment varied widely among crops and experiment conditions, and the effects of CO_2 enrichment on PNC may be strongly influenced by plant species and environmental factors (Fernando et al., 2012; Kanowski, 2001; Murray et al., 2000). In detail, the PNC of P was increased under atmospheric CO_2 enrichment in rice (*Japonica* cv. Wuxiangging 14) (Yang et al., 2007), in *S. secundatum* (Edwards et al., 2006), and in barnyard grass (Zeng et al., 2011) or remained unchanged in *Alphitonia* (Kanowski, 2001), *Vigna* radiata (Li et al., 2015). Likewise, the PNC of K was increased in rice and barnyard grass (Zeng et al., 2011) unchanged in *Alphitonia* (Kanowski, 2001) and in *Vigna* radiata (Li et al., 2015) but reduced in *Flindersia* (Kanowski, 2001) under CO_2 enrichment. In this study, the supply of P and K as in fertilizer input was relatively high compared to that of N (*i.e.* the nutrient percentage of the N-P-K compound fertilizer used). Likely, CO_2 enrichment unchanged the PNC of P and K in conditions of enough exotic fertilizer supply in the rice paddy.

Overall of PNC and biomass production, the nutrient accumulation under CO_2 enrichment in the ripening stage was not significant difference between CE and CK treatments (Fig. 3). Apparently, there could be tradeoff between the change in plant concentration and the change in the biomass production under CO_2 enrichment (Roy et al., 2012; Sakai et al., 2006). Of course, atmospheric CO_2 enrichment led to a higher plant biomass in both years (Fig. 1b). Consequently, the NUE of remained promoted for N and K but not for P under CO_2 enrichment (Table 1), indicating that CO_2 enrichment exerted a slight but significant effect on the NUE of N and K reasonably with the slightly but significantly stimulated grain yield (Fig. 1a). Therefore, improving N and K nutrient supply could be an attainable approach for negating climate change impacts on rice production.

4.2. Warming effect on nutrient uptake and accumulation

In this study, canopy warming increased PNC of P and K generally across growth stages in 2013 but mostly unchanged in 2014 (Fig. 2 & Table 2). This seemed contrast to the changes under CO_2 enrichment, which was more often with N and likely in 2014. Under warming, the PNC of N was more or less increased in both years. As reported by Kim et al. (2011) for rice, warming could increase plant aboveground N concentration, due mainly to enhanced soil nutrient mineralization (Rustad et al., 2001). In the experiment, warming caused an increase in microbial biomass carbon (Wang et al., 2016b), which could indicating higher microbial mineralization ability. Additionally, the changes in the PNC of P and K in rice plant here could be ascribed to increased leaf transpiration under warming condition (Jauregui et al., 2015). As noted by Trenberth et al. (2005), higher air temperatures could increase leaf surface temperatures and thus the vapor pressure deficit, which increased leaf transpiration rates, nutrient translocation from belowground, and nutrient accumulation in plant tissues. Previous studies also found that warming increased leaf transpiration for rice and promoted element translocation from belowground to aboveground (Ge et al., 2016; Wang et al., 2018).

Despite the increment of P and K concentrations under warming condition, the PNA of N, P and K were all decreased in 2013. This could be attributed largely to the reduction in biomass production under canopy warming. Warming stimulated plant respiration and accelerated phenological development, and thus led to lower biomass production (Dong et al., 2011; Nagai and Makino, 2009). Additionally, Eichelmann et al. (2011) also demonstrated that the inhibitory effect of elevated temperature on plant respiration decreased the energy required for nutrient assimilation. In this study, the decrement by 5.4–20.3% for grain yield and 6.2–26.2% for aboveground biomass were also observed under warming alone (Fig. 1). However, the PNA seemed unchanged in 2014 under warming alone (Fig. 3). Differential responses of nutrient to canopy warming in 2013 and 2014 may be due to different weather conditions (e.g. mean daily temperature of 27 °C in 2013 *vs.* of 24.2 °C in 2014). Some studies also suggested that warming showed negative effect on crop growth in warm south China (Wang et al., 2016a), but no effect or even a positive effect in cold region (Cheng et al., 2010). Therefore, the negative effect of warming on nutrient accumulation could be weakened in years of lower temperature.

4.3. Interactive effect of CO_2 enrichment and warming

Results of this study showed that CO_2 enrichment was unable to compensate for the adverse impact of warming on the PNA of N and K in both years (Fig. 3a, c). A number of factors were shown to be generally responsible for the significantly negative effects of CW on the PNA of N, P and K. Firstly, being most important, warming reduced biomass accumulation due to increased plant respiration and shortened crop phenological development as well as inhibited nutrient assimilation, indirectly reduced total nutrient accumulation under concurrent CO_2 enrichment and warming (Jauregui et al., 2015; Wang et al., 2016a). Secondly, higher temperature increased plant cell permeability, which enhanced potassium ion loss (Taiz and Zeiger, 2006). Thirdly, CO_2 enrichment increased soil microbial biomass (Wang et al., 2016b), and stimulated microbial activity and reproduction when combined with warming in paddy field (Liu et al., 2015; Okada et al., 2014). This may cause a competition for nutrients with plants under concurrent CO_2 enrichment and warming in the paddy field. However, inter-annual variation in N and K uptake was observed in this study. It has been reported that inter-annual variability of crop production in the experimental site was associated with the inter-annual change in air temperature (Wang et al., 2016a). The mean daily temperature of the second year (24.2 °C) was lower than that of the first year (27 °C). This indicates that the offsetting effect of warming on positive biomass response to CO_2 enrichment may not be significant under a higher temperature, and that the effect of concurrent CO_2 enrichment and warming is not simply a cumuli addition of their individual effects.

The changes in NUE of N and K under concurrent CO_2 enrichment and warming condition were greater than that under atmospheric CO_2 enrichment alone, but in contrast to a negative change under warming alone (Table 1 & Fig. 4a, c), indicating that warming tended to accelerate the negative response of PNA to CO_2 enrichment. In consistence with the finding by Jauregui et al. (2015), who has found that warming inhibited the activities of nitrate reductase, glutamate synthetase and dehydrogenase and in turn reduced plant N assimilation for wheat when simultaneously exposed to CO_2 enrichment. Concurrent CO_2 enrichment and warming caused a decline in nutrient transport for wheat due to the decreased leaf transpiration (Cammarano et al., 2016; Jauregui et al., 2015). Furthermore, our study showed that concurrent CO_2 enrichment and warming had no effect on grain yield in both cropping seasons (Fig. 1a), while greatly decreased respectively PNA of N and K by a mean of 12.9% and 16.2% over two years (Fig. 3a, c), result in increases in NUE of N and K under concurrent CO_2 enrichment and warming compared with CK. The increase in NUE of N under concurrent CO_2 enrichment and warming was also found in other rice paddy studies (Nam et al., 2013; Roy et al., 2012). However, concurrent CO_2 enrichment and warming had no effect on the P uptake and utilization efficiency compared with CK in present study (Fig. 4b). This contrasts with the finding by Bhattacharyya et al. (2014), who reported that the P uptake by rice at a rate of 40 kg P_2O_5 ha^{-1} was significantly increased by concurrent CO_2 enrichment (550 ppm) and warming (+2 °C) under an open-top chamber experiment from India. This contrasting effects between CO_2 enrichment and warming may be explained by the different experimental conditions and fertilizations. This indicates that nutrient cycling under future simultaneous atmospheric CO_2 enrichment and warming are more complex than under either CO_2 enrichment or warming alone. Therefore, further studies are needed to investigate the nutrient metabolism mechanisms under concurrent CO_2 enrichment and warming for better crop adaptation to future climate.

5. Conclusion

Changes in PNC, PNA and NUE by rice were not consistent among elements and across climate change treatments and years in an open field experiment of fertilized rice paddy. CO_2 enrichment slightly decreased PNC at some stages, but unchanged PNA despite of a CO_2 fertilizer effect on biomass production. In contrast, canopy warming increased PNC whereas decreased PNA and altered the responses of NUE of N and K to CO_2 enrichment in both years. As for the open air field experiment with simulated CO_2 enrichment up to 500 ppm and canopy warming by 2 centigrade, warming even accelerated the potential negative effect by CO_2 enrichment on nutrient uptake and use efficiency for rice. Therefore, improving nutrient supply should be pursued in order to better adapt rice production systems to climate change in the future.

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